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INHERITANCE OF THE "EYE" IN VIGNA

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CERTAIN races of the cowpea (*Vigna unguiculata*) have the seed coat completely pigmented, others have no pigment, while others have pigment confined to certain areas. In this paper the fully pigmented races are referred to as having solid color, those without pigment as white, while the pigmented area of the partially pigmented seed coats is called the "eye." This eye, when small, is always confined to the region of the hilum, and when large always surrounds the hilum. It varies widely in size and form, as shown in the accompanying illustrations, which show the principal types of eye. In *a* the pigmented area is confined to two patches on opposite sides of the hilum. In *b* the area surrounds the hilum except at its micropylar end.

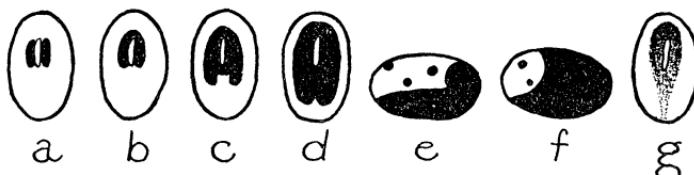


FIG. 1. Forms of the "eye," or pigment area, in the seeds of the cowpea.

In *c* the hilum is completely surrounded, but there is a broad indentation at the lower end of the pigmented area. In *d* the eye covers nearly the entire ventral¹.

¹ The terms ventral and dorsal are used in this paper to describe respectively the side of the seed showing the hilum and the opposite side.

surface of the seed, but has a characteristic notch at the micropylar end (lower end in the figure). In *e* the area has extended over the micropylar end of the seed. In this form and the next there are usually some isolated spots of pigment in the non-pigmented area. In *f* the pigmented area covers all except the dorsal portion of the chalazal end of the seed. Between the forms *a* and *f* there is nearly a complete series of connecting links represented in the material in my possession, but in the present paper I shall not attempt to deal with this whole series, because the genetic relation between some of its members is not yet worked out. Forms *a-c* will here be considered as one, under the name ordinary eye or small eye. Forms *e* and *f* will be treated as one, under the name Holstein, from the color pattern of a variety having this name. The evidence thus far available indicates that form *d*, which is here called large eye, is always heterozygous between Holstein and small eye. Perhaps other of these forms of eye are also heterozygous; material which it is hoped to obtain from the crop of 1911 (F_3) will probably determine this point. There is some evidence that forms *a*, *b* and *c* are the DD, DR and RR of a Mendelian pair. The same is probably true of *e* and *f* and a type intermediate between them. Form *g* of Fig. 1 represents a genetically distinct type of eye. In it the pigmented area surrounds the hilum, but the micropylar end of the area has the margin very indistinct; fine dots of pigment extend over the micropylar end of the seed. In races of this type that are black pigmented the pigment extends over the whole surface of the seed, but it is much denser in the region of the eye than elsewhere. The reduced pigmentation in such cases varies from very dark, rendering close inspection necessary to detect the eye, to very pale, making the eye as conspicuous as it is in buff or red pigmented races. Whether these variations in intensity of pigmentation have genetic significance is not yet determined, but investigations now in progress will, it is hoped, settle this point. This type of eye, in which an ill-defined area of pigment extends over the micropylar

end of the seed (see *g*, Fig. 1), is here called the Watson Eye, from a variety known as Watson's Hybrid, which has this type of eye. This variety, as well as the Holstein variety, is said to have originated from crosses between black varieties and Black Eye. My investigations show that both these color patterns occur in the second generation of all crosses of this kind, as will be seen later, thus confirming the supposed origin of both these varieties.

The Watson type of eye has not heretofore been recognized. But since the essential difference between it and other eye types was noticed, the writer has found in the collection of cowpea varieties in the office of the agrostologist several races having this type of eye. The existence of this type was discovered as a result of the discovery that in several crosses between eyed and completely pigmented races the ratio of fully pigmented to individuals with eyes in F_2 was 3:1 in certain cases and 9:7 in others. The latter ratio suggested that two genetically distinct types of eye were present in certain crosses. A careful study of the rather extensive material at hand revealed the types of eye already described, and a tabulation of the statistical data relating to the inheritance of each of them revealed the relations between these types which are discussed in this paper.

STATISTICAL DATA

Cross: Small Eye \times Solid Color (fully pigmented)

In all, 21 crosses of this kind were made. In all cases F_1 was solid color. It happened that in classifying the individuals of the F_2 generation, before the types of eye present were fully recognized, Large Eye and Small Eye individuals were not separated in 5 of the 21 families. In the remaining 16 families, taken together, the proportion of the various types of color pattern in F_2 was as follows:

	Solid Color	Watson Eye	Holstein	Large Eye	Small Eye
Number of individuals in the 16 families taken together	127	41	12	34	12
Highest expectation	126	42	14	28	14

on the assumption that the ratio between these various types is 9:3:1:2:1. The reason for assuming this ratio will be given later.

In the 5 families in which the large and small eyes were not separated, and in which the corresponding expectation is the ratio 9:3:3:1, the results were:

	Solid Color	Watson Eye	Holstein	Large and Small Eye
Number of individuals in 5 families taken together	100	30	34	16
Highest expectation	101	34	34	11

In both these groups the actual numbers are in close accord with the theoretical numbers called for by the assumed ratios.

Cross: Holstein × Solid Color

Six crosses were made between various types of the Holstein pattern and solid-colored races. The F_1 plants all produced seeds that were fully pigmented. In F_2 , taking the six families together, there were 75 individuals bearing fully pigmented seeds and 25 with Holstein seeds, or exactly the ratio 3:1.

Cross: Watson Eye × Solid Color

Two of the 4 Watson parents used in these matings proved to be heterozygous. The other two, taken together, gave 56 solid color and 13 Watson individuals in F_2 . F_1 in all these cases was fully pigmented. The 3:1 ratio for the number of individuals in F_2 is 52:17, which agrees fairly well with the experimental results.

Cross: Small Eye × Holstein

Only one cross of this character was made. It gave F_1 with large eye; in F_2 there were 3 Holstein, 4 Large Eye and 1 Small Eye individuals, which is near the ratio 1:2:1 for these three types of color pattern.

MENDELIAN FACTORS INVOLVED

We may bring together here the various ratios found in the above classes of matings. For convenience let us designate the various color patterns as follows:

S = Solid color (fully pigmented seed coat).	
W = Watson Eye.	
E = Small Eye.	
LE = Large Eye.	
H = Holstein.	
Crosses	Ratios
E × S	9:3:1:2:1 or 9:3:3:1.
H × S	3:1.
W × S	3:1.
E × H	1:2:1.

These ratios point clearly to the following conclusions:

1. Types E and S differ from each other in two factors each of which exhibits the phenomenon of dominance or partial dominance.
2. Types H and S differ in one factor which shows dominance.
3. Types W and S differ in one factor which shows dominance.
4. Types E and H differ in one factor, the heterozygote being intermediate between the parental types.

It is not difficult to formulate, in terms of the customary hypothetical factors, an hypothesis that readily explains these facts. In fact, I have been able to formulate four such hypotheses. In each of these a certain set of factors is assumed, each factor being assumed to have the power of producing a particular effect on the color pattern of the seed coat. But such explanations offer no suggestion as to the real nature and *modus operandi* of these factors. Unfortunately we do not know much concerning the complex chemical processes that go forward in the living cell. But enough is known to show that differences such as are exhibited by the various color patterns here considered may be due to some such cause as slight difference in the rate at which some enzyme may be produced in the cells of the seed coat. For instance, it is known that an enzyme may cause certain sugars and chromogens to unite to form a glucoside, thus removing the chromogen from the sphere of action of an oxidizing enzyme that might con-

vert it into pigment.² Another enzyme, or, under appropriate conditions, the same enzyme that brought about the synthesis of sugar and chromogen into glucoside, may hydrolyze glucoside into sugar and chromogen. It is also known that the rate at which a chemical reaction determined by an enzyme goes forward depends on the amount of enzyme present. It is therefore readily seen that the rate at which a given enzyme is produced in the cell may determine whether or not chromogen shall be available for conversion into pigment. It is also highly probable that a principal function of the chromatin of the cell is to produce the enzymes which govern at least the rate of many of the metabolic processes in the cell.³

It is certain that environmental conditions during ontogeny determine whether pigment shall be produced in a given tissue, even when the potentiality of pigment production is known to be present. Thus, in seeds that have pigmented coats, pigment may not occur, say in the endosperm. Causes similar to those which determine the particular tissue to be pigmented may also determine what portion of that tissue shall be pigmented. The sugar in the pigment cells of the seed coat is presumably transported there by osmosis from cells some distance away. Other materials necessary to the reactions may be brought from other parts of the organism, and some of the products of a reaction the accumulation of which might retard the reaction may be transported to other parts of the organism as they are produced. We thus have to deal with an exceedingly complex problem, many of the elements of which can not even be conjectured in our present ignorance of cell metabolism. It would therefore be idle to attempt to formulate a definite theory of the processes involved. A slight change in the permeability of certain cell walls, a change in the size of certain cells, the substitution of

² "On the Formation of Anthrocyanin," M. Wheldale, *Jour. of Gen.*, I, No. 2.

³ Guyer, M. F., "Nucleus and Cytoplasm in Heredity," *AMER. NAT.*, May, 1911.

a slightly different group of atoms for a single side chain in a molecule of chromatin or one of the constituents of chromatin, or any one of numerous other changes, might determine whether pigment is to be formed in a given cell, or whether it may be produced at all. But if the change which is responsible for the difference between two related organisms is a change in any permanent organ of the cell, then the difference in question will be hereditary. If it occurs in the material of a chromosome, or any other cell organ that behaves as a chromosome does in the reduction division, the difference in question will Mendelize.

Let us suppose, merely for purposes of illustration, that the difference between fully pigmented seed coat and the Holstein coat pattern is due to a difference in the rate at which a particular chromosome manufactures a particular enzyme under given conditions. Then when these two patterns are crossed we should get the usual phenomena of monohybridism, with the ratio 3:1 (or 1:2:1). Thus the Holstein pattern is not necessarily due to the "loss" of a "factor"; it may be due to some such cause as a difference in the quantity of an enzyme produced by a particular chromosome. The use of such expressions as "presence of a factor" and "absence of a factor" in what follows is therefore not meant to imply the presence of a morphological entity in one race and its absence in another. It rather means that in one race some cell organ, probably a chromosome in Mendelian inheritance, performs a certain function differently, or under different conditions, in the two races. Since the phenomena of Mendelian inheritance point clearly to the physical behavior of some cell organ, I prefer to think of the symbols used in expressing the genetic constitution of a type as representing the bodies, differences in the functions of which give rise to the character "pair."

Thus the symbol W in what follows may be considered as representing a cell organ which, under certain conditions, performs a certain function in such a way as to account for the difference between Small Eye and Wat-

son Eye, while w represents the same cell organ, or rather the corresponding organ, in another variety, which does not perform this same function in the same way under similar conditions. The symbol w need not imply that the power of performing any function is lost. It is here meant to imply only that the function is not performed in such manner as to produce the effect that W would have produced had it been present. Another way of putting it is that W represents a function performed, while w represents that the function is not performed. With this understanding of what is meant by a Mendelian "factor," we may proceed to examine the hypotheses which explain the statistical results given above.

The behavior of the cross: small eye \times solid color indicated that these two types differ in two factors which are transmitted independently of each other. Let us represent these factors as they appear in fully pigmented peas by W and H , and in small-eyed peas as w and h . This implies, according to my conception of Mendelian factors, that some cell organ (W), probably a chromosome, performs a certain function in certain races of peas that is either not performed, or is performed differently, by the corresponding organ (w) in another race of peas. A similar remark applies to H and h . With reference to these two factors, the formula of fully pigmented peas may be written $WWHH$, and of small-eyed peas $wwhh$. We have already seen that the Holstein type differs from the type with small eye in one factor; also from fully pigmented in one factor. Hence it must have either the formula $WWhh$ or $wwHH$. That is, in one of the two factors concerned it is like Solid Color, in the other, like Small Eye. We may therefore take $wwHH$ as the formula of the Holstein type. In an exactly similar manner we arrive at the formula $WWhh$ for the Watson type. We may bring these formulæ together for purposes of comparison.

- (1) Solid Color : $WWHH$.
- (2) Watson Eye : $WWhh$.
- (3) Holstein : $wwHH$.
- (4) Small Eye : $wwhh$.

These formulæ give the ratios previously assumed in dealing with our statistical data for the F_2 generation, provided we assume W and H dominant respectively to w and h.⁴ An interesting deduction from them is that the cross between the Watson and the Holstein types should give the same ratio in F_2 ; namely, 9:3:1:2:1, that the cross between solid color and small eye gave. In the original crosses, the cross Holstein \times Watson was not included, but it is included in crossings now being made.

These formulæ give some hint as to the nature of the effect produced by the factors W and H. Comparing (4) and (3), the factor H has the effect of enlarging the pigmented area from the small eye type to the Holstein type (see *b* and *e*, Fig. 1). Comparing (2) and (4), W is seen to have the effect of enlarging the pigmented area of the Small Eye type, changing it to the Watson type (see *g*, Fig. 1). W and H together, even in the hybrid $WwHh$, have the effect of spreading pigment over the whole seed-coat.

We have seen that the heterozygote between Holstein and Small Eye, which has the formula $wwHh$, is intermediate between the parent forms. In earlier pages this type has been designated Large Eye. It therefore appears that H duplex enlarges the pigment area about twice as much as H simplex does. Whether the same is true of the factor W has not yet been determined. As the ratio 9:3:1:2:1 is somewhat unusual, it may not be out of place to illustrate the manner of its occurrence. In the cross: Small Eye \times Solid Color, F_1 has the formula $WwHh$, and is solid color. Generation F_2 is as follows:

F_2 OF THE CROSS SMALL EYE \times SOLID COLOR.			$= wwhh \times WWHH$	
	Solid Color	Watson	Holstein	Large Eye
1	WWHH	1	—	—
2	WWHh	2	—	—
1	WWhh	—	1	—
2	WwHH	2	—	—
4	WwHh	4	—	—
2	Wwhh	—	2	—
1	wwHH	—	—	1
2	wwHh	—	—	2
1	wwhh	—	—	—
		9	3	1
				2
				1

⁴The dominance is only partial in the case of H and h.

Should it later prove possible to separate the two Watson F_2 types, $WWhh$ and $Wwhh$, as we can the corresponding Holstein types, we should then have the interesting ratio 9:1:2:1:2:1.

There is evidence in my material that the Holstein and Small Eye types are still further influenced by one or more additional factors. This matter is now under investigation. These additional factors appear to act in a manner entirely similar to the factor H, but have less effect. Taking the formula for Small Eye and adding a factor I, similar in effect to H, we should have the three types $wwhhII$, $wwhhIi$, and $wwhhii$, all three of which appear to be distinguishable, giving probably the three types *a*, *b* and *c* of Fig. 1. This point will be studied in F_3 of the original crosses, of which a vast quantity of material is growing, as well as in new crosses now being made.

OTHER HYPOTHESES

In the above hypothesis the factors W and H were assumed to have the property of enlarging the pigmented area. The facts can also be explained by assuming that w and h have the power of reducing the pigmented area. In fully pigmented races, on this hypothesis, these factors are absent. When w is introduced the pigmented area is reduced to the Holstein pattern. h, without w, reduces it to the Watson pattern, while w and h together produce the Small Eye pattern. It is necessary in this case to assume W and H dominant, respectively, to w and h, as in the first hypothesis.

We may also assume a factor W for Watson Eye, a factor, E, allelomorphic to W, for Small Eye, and a third factor, S, which tends to enlarge the pigmented area, converting Small Eye into Holstein, and Watson Eye into Solid Color. Here, W must be epistatic to E. Under these assumptions the formulæ of the principal color patterns would be:

Solid Color	:	WWSS.
Holstein	:	EESS.
Watson	:	WWss.
Small Eye	:	EEss.

A fourth hypothesis is as follows:

H = a factor for Holstein pattern.

E = a factor for Small Eye pattern.

S = a factor which enlarges the pigmented area, converting E into Watson, and H into Solid Color.

H is here epistatic to E.

All four of these hypotheses are in complete agreement with the statistical data, and lead to exactly the same types, and the same ratios, in all generations.

If we look upon the symbols as representing cell organs, differences in whose functions are responsible for the phenomena observed, then these four hypotheses are identical. They all provide exactly the same set of cell organs. The differences between the hypotheses are found only in the nature of the functions which these cell organs are supposed to perform. As we know nothing definite about these functions, the hypotheses are essentially identical within the range of present knowledge. The functions assumed for the bodies represented by the symbols of the first hypothesis seem to the writer to accord more nearly with our meager knowledge of cell chemistry.

The author desires to acknowledge his indebtedness to Mr. G. W. Oliver, who not only performed the cross-fertilizations planned by the writer, but freely made available similar extensive material of his own, which is included with my own in these studies. Mr. Oliver also grew the F_1 hybrids. He is also under obligations to Mr. J. W. Froley, Mr. E. D. Carmack and Mr. W. R. Humphries, who grew the F_2 plants and made the necessary field notes; to Mr. E. P. Humbert, who rendered valuable assistance in classifying the F_2 material, and to Professor C. V. Piper, agrostologist of this bureau, who furnished seeds of the varieties used as parents in these investigations, and made many helpful suggestions concerning probable "factors" present in the varieties.